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Root characteristics of selected field crops: Data from the Wageningen Rhizolab (1990–2002)

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Abstract

Since being built in 1990, the rhizotron facility in Wageningen, the Wageningen Rhizolab, has been used for experiments on crops (e.g. Alfalfa, Brussels sprouts, common velvet grass, field bean, fodder radish, leeks, lupins, maize, potato, beetroot, ryegrass, spinach, spring wheat, winter rye and winter wheat). In the experiments, horizontal glass minirhizotron tubes combined with auger sampling were used to assess rooting characteristics. For this paper we took the root data from these experiments and looked for a general relationship between thermal time/time after planting and rooting depth, the velocity of the root front and root proliferation. For certain depths (fixed by the depth at which the horizontal minirhizotrons were installed) a simple linear regression was established between the average root number per cm^2 minirhizotron surface area and thermal time after planting. The compartments selected for each crop were those in which there had been a control treatment and/or in which conditions for rooting were considered to be optimal. We performed regression analyses per compartment and per depth, but only for the period after planting in which a linear increase of root numbers vs. thermal time was observed. After averaging the results, the regression procedure yielded two parameters of rooting for each crop: (a) the actual or thermal time at which the first root appeared at a certain depth and (b) the root proliferation rate after the first root had appeared. In this way, inherent crop differences in rooting behaviour (rooting depth and root proliferation) became apparent. For each crop, the 'velocity of the root front' after planting could be established (calculated in cm (°C day)$^{-1}$). This parameter differed greatly between crops. Some crops (such as leeks and common velvet grass) explored the soil profile slowly: the root front moved at a velocity of only 0.07 cm (°C day)$^{-1}$. Among the crops whose roots grew down much faster (0.18–0.26 cm (°C day)$^{-1}$) were cereals and fodder radish. For a day with an average temperature of 15 °C these rates would have corresponded with the root front travelling approximately 1–4 cm per day. In the crops studied the root front velocity did not correlate with the root proliferation rate.

Introduction

There are various reasons why knowledge about rooting characteristics such as rate of root proliferation and rooting depth is crucial if the efficiency of modern cropping systems is to be optimised: –Water availability determines crop performance, particularly in environments where water supply is variable and limiting. Given that a crop's ability to extract water depends largely on the depth and uniformity of its root system (Dardanelli et al., 1997), root penetration rate and rooting depth are factors to consider when selecting a crop that will effectively use the reserves of water in the soil (Stone et al., 2001). Crops whose roots penetrate the soil fast and deeply are better able

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to avoid drought because they can use water from deeper soil layers.

– Nutrient availability and crop performance are related to rooting in more or less the same way as water availability. The volume of soil a crop's roots can explore and exploit for nutrients depends largely on the crop's rooting depth and rooting intensity, especially if the soil nutrients are immobile.
– A final point is the direct relationship between rooting characteristics and nutrient use efficiency. The undesired leaching of nitrogen to groundwater is especially likely to occur in profiles with a coarse sand texture and with a shallower rootable depth (Bowman et al., 1998). In this situation, rooting depth seems more important than rooting intensity, as low rooting densities (1 cm cm^{-3}) are sufficient to take up the crop's daily nutrient requirements (de Willigen and van Noordwijk, 1987).

Smit et al., (1995) and Smit and Zuin (1996) concluded that the main reason for the low nitrogen use efficiency of leeks was not the low rooting intensity of this crop but the shallow rooting in combination with periods of low rates of nitrogen uptake. Indeed, it is precisely the rooting depth potential that is important for the success of the nitrogen catch crops used to prevent the residual nitrogen from a previous crop being leached out in the winter (Thorup Kristensen, 1993a, 2001). On the basis of simulation experiments, Thorup Kristensen and Nielsen (1998) concluded that the effect of catch crops on the nitrogen availability for the following crop also depends on the following crop's rooting depth.

Rooting depth can be considered as an inherent crop characteristic. Some crops (leeks, spinach) root shallowly, others (sugar beet, wheat, etc.) root deeply. However, the rooting depth of an individual crop can be influenced strongly by local conditions. Examples of local soil factors that affect rooting depth (and thus nitrogen leaching, nitrogen use efficiency, etc.) for a specific site are soil compaction or bulk density (Dracup et al., 1992; Unger and Kaspar, 1994), and soil pH (Rechcigl et al., 1987).

During the first 10 years of operation of the Wageningen Rhizolab, root data were collected in experiments with various crops that examined a variety of research questions, ranging from the effect of enhanced levels of CO_2 on root growth to the effect of nematodes on crop growth and nutrient uptake. In this rhizotron facility, crops are grown in compartments that have been filled by hand as uniformly as possible and at a specific bulk density. The root development in most of the compartments can be assumed to indicate the root development that would occur in conditions where the crop has no constraints to rooting (potential rooting pattern). For a detailed description of the experimental conditions in the rhizotron facility, see Smit et al. (1994).

The data presented in this paper can be used to calibrate or validate the various types of models for simulating root growth (see Asseng et al., 1997). Many of these model root growth by first calculating potential root growth (the root growth achieved under optimal conditions) and then applying correction factors for factors constraining rooting, such as pH, bulk density, water table, water availability and nutrient availability. For example, Heinen et al. (2003) described root growth by a diffusion equation with a diffusion coefficient D, and proposed to simulate the effect of wet or dry regions on root growth by making the diffusion coefficient a function of pressure head of the soil with a simple reduction factor. An approach to root growth that takes more account of plant physiology (based on the functional equilibrium between shoots and roots) has been incorporated in models in which root growth is dependent on the carbon supply to the roots (e.g. Asseng et al., 1997). Both approaches, however, need benchmark data on root growth under optimal conditions, so that the influence of factors constraining root growth can then be calculated.

Roots are crucial in crop models simulating water movement or nutrient transport (including leaching). For example, after analysing the sensitivity of the STICS crop simulation model, Ruget et al. (2002) concluded that yield depended on all the modules (shoot, soil and rooting modules) whereas other outputs (e.g. water uptake, drained water and leached nitrogen) depended mainly on the water balance and rooting modules. In general, therefore, a reliable prediction of the spatial distribution of root growth in time seems crucial for modelling water and nutrient uptake and nutrient transport.

Using data from the Wageningen Rhizolab on various crops we investigated potential and actual rooting depth as a function of actual and thermal time, as well as root proliferation as a function of thermal time and depth. The data we present can be used to improve models to predict root growth under various conditions. But even without using models, the data can be used to predict how fast a specific crop can explore the soil profile with respect to water and nutrient uptake. Furthermore, the information in this article on rooting will be helpful when developing environmentally friendly fertilisation strategies such as split nitrogen applications and placement of nitrogen, especially in the case on soils prone to leaching, where rooting characteristics can affect nitrate leaching.

Materials and methods

The Rhizolab facility

The Wageningen Rhizolab, a rhizotron facility, was set up in 1990 (Van De Geijn et al., 1994). It consists of two rows, each with eight below-ground compartments aligned along a corridor. When it starts raining, a shelter automatically covers the experimental area. The compartments are 125 cm by 125 and 200 cm deep. On four compartments a transparent enclosure allows that canopy photosynthesis, respiration, and transpiration can be measured. The root data we used are from experiments with repacked soil. The compartments were filled by hand, and compacted layer by layer (5 cm) to a bulk density of approximately 1.3–1.4 g cm^{-3} throughout the profile. In most experiments the profile of the compartments consisted of a metre of humic sandy soil (1.5–4% organic matter), overlying a metre of coarse sand (with no organic material) that roots did not penetrate. In some experiments the humic part of the profile was only 60 cm deep.

Experiments

Table 2 presents the following information for each experiment (grouped by crop): date of planting, date of harvest, elapsed # of days and thermal time until harvest, plus brief details of the experimental treatments. Data from experimental treatments that influenced the rooting pattern (e.g. drought, CO_2 concentration, nematode infection) were excluded from this study; instead, only data from the control treatments were used. Table 2 gives information about the conditions in these control compartments. Table 2 also gives details of any available references that contain more experimental details and results.

From the planting and harvesting dates and the thermal time that had elapsed by the end of the experiments it is clear that normal growing periods occurred in most experiments and that crops were allowed to grow until mature or until a normal yield had developed. Only the maize experiments focused on nitrogen uptake in the early stages of crop development and were therefore harvested early.

Observations

Root number. Roots in the Wageningen Rhizolab were observed using two methods: (a) non-destructive, using horizontal, glass minirhizotrons at intervals of 14 days between observations; (b) destructive sampling using augers on three dates in the season (Smit et al., 1994). Here, we present the data collected with minirhizotrons, per depth, as the number of roots per cm^2 of the glass surface of the minirhizotron. This is the average root number observed in approximately 35 images (18 × 13 mm each) taken at the top of the minirhizotrons. For further details on observation protocol and the relationship between the number of roots per cm^2 minirhizotron surface and the root length density (in cm cm^{-3}) as assessed with auger sampling, see Smit et al. (2000b, 1994). If it is assumed that the direction of root growth is random, the volumetric root length density ($L_{rv,z}$, in cm cm^{-3}) at depth z can be estimated (Melhuish and Lang, 1968) from the number of roots cm^{-2} ($N_{r,z}$) at that depth as:

$$L_{rv,z} = 2^{*} N_{r,z} \tag{1}$$

This relationship is generally valid for most of the root data collected in the Rhizolab, but is not always valid for all stages of crop growth (Smit et al., 1994). See also Table 1.

Root proliferation (*increase in root number*). In most experiments the minirhizotrons were at depths of 5, 10, 15, 20, 30, 45, 60, 80 and

Table 1. Details of symbols used

	Description	Dimension
L_{rv}	Volumetric root length density	cm cm^{-3}
$N_{r,z}$	Number of roots per cm^2 minirhizotron surface at depth z	cm^{-2}
$N_{r,z,el}$	The number of roots per cm^2 minirhizotron surface at the end of the linear phase (root number vs. thermal time) at depth z	cm^{-2}
$N_{r,z,m}$	The maximum number of roots per cm^2 minirhizotron surface during the experiment at depth z	cm^{-2}
$T_{r,z,0}$	Thermal time after planting at which the first roots arrive at depth z (= intercept at the x-axis when $N_{r,z}$ (y) is regressed on thermal time (x))	°C day
$T_{r,z,0.5}$	Thermal time after planting at which root number was 0.5 cm^{-2} minirhizotron surface at depth z	°C day
$\Delta N_{r,z,l}$	the rate of increase of root number with thermal time at depth z (in the linear phase)	(°C day)$^{-1}$

100 cm, and each tube was observed at 14-day intervals. For each observation series (depth per compartment) we assessed the period after planting in which the increase in $N_{r,z}$ was more or less linear. For each depth z we recorded the number of roots at the end of this linear phase ($N_{r,z,\ el}$) and performed a linear regression on root numbers vs. thermal time (base temperature 0 °C). Thermal time was used to allow a better comparison between and within years. The explained variation was usually well above 95%. The slope of the regression line reflects the increase in root number at depth z ($\Delta N_{r,z,l}$) after the first roots had reached that depth, i.e. the root proliferation at that depth.

In most cases, the roots proliferated more slowly after the linear phase, until a maximum ($N_{r,z,m}$) was reached. Root number then decreased – especially at shallower depths – due to root die-back. However, deeper in the profile the root number usually achieved a maximum at the end of the experiment.

Thermal time needed for roots to arrive at a certain depth ($T_{r,z,0}$). Using the regression equations of root number (y) vs. thermal time (x) mentioned above we calculated the intercept with the x-axis. For a certain depth–crop combination this intercept ($T_{r,z,0}$) can be considered as the thermal time at which the first roots (the 'root front') arrived at that particular depth.

Thermal time needed for a root number of 0.5 cm^{-2} ($T_{r,z,0.5}$). The regression equations allowed us also to estimate the thermal time needed at a certain depth to arrive at a $N_{r,z}$ of 0.5 cm^{-2} ($T_{r,z,0.5}$). This value of 0.5, assuming equation (1) is applicable, would correspond to a volumetric root length density ($L_{rv,z}$) of 1. According to de Willigen and van Noordwijk (1987), at this particular root length density the root length would not limit nitrogen uptake for most conditions. The shorter the period from planting to $T_{r,z,0.5}$ the shorter the period that roots would constrain nutrient uptake at that depth, which is an important characteristic for most plant species grown as crops. It must be kept in mind that this paper focuses on the period after planting in which the increase in root number with thermal time is more or less linear. The calculated regression equations were used for prediction within this linear phase, but should not be used for extrapolation to later stages, as the results would be unreliable.

'Root front' velocity. Finally, for each crop we performed a separate linear regression between depth (z) and the average thermal time the first roots arrived ($T_{r,z,0}$) at that depth. For nearly all crops this relationship was linear. The slope of the regression line reflects the velocity of the 'root front' (in cm (°C day)$^{-1}$).

Statistical aspects. In most of the crops, using data from the control compartments resulted in a number of independent replicates (see column 2 of Table 2). We calculated the average and standard deviation of observations (maximum root number, DAP when first roots arrived, etc.) for each crop and each depth.

Table 2. Details of the experiments in Wageningen Rhizolab from 1990 to 2002

Experiment #	Crop	Compartment #	Date of planting	End date	No. of days	Thermal time at the end of exp.	Experimental factors varied in the experiment	Treatment in control compartments	References/comments
31	Alfalfa (*Medicago sativa* L.)	8	29-Apr-98	2-Dec-98	218	2794	Phytoremediation of a kerosene spill	No kerosene	(Hwu and Grotenhuis, 2001; Smit et al., 2000b)
7	Brussels sprouts (*Brassica oleracea* L. *var. gemmifera*)	10	30-May-91	26-Nov-91	183	2415	Nitrogen level	200 kg N short period with no water	(Smit et al., 1995; Smit et al., 1996; Smit and Zuin, 1996)
7	Brussels sprouts (*Brassica oleracea* L. *var. gemmifera*)	12	30-May-91	26-Nov-91	183	2415	Nitrogen level	100 kg N short period with no water	(Smit et al., 1995; Smit et al., 1996; Smit and Zuin, 1996)
32	Common velvetgrass (*Holcus lanatus*)	4	18-Jun-98	6-Nov-98	142	1982	PAC-amended soil	Anthracene and pyrene (but no effect on growth); profile 60 cm	see also (Fransen and De Kroon, 2001) for another experiment
9	Field bean (*Vicia faba* L.)	1	3-Apr-92	7-Sep-92	158	2415	CO_2 level	350 ppm CO_2 Crop in growth chamber	(Dijkstra et al., 1996; Grashoff et al., 1995)
9	Field bean (*Vicia faba* L.)	5	3-Apr-92	7-Sep-92	158	2415	CO_2 level	350 ppm $CO_{2;}$ Crop in growth chamber	(Dijkstra et al., 1996; Grashoff et al., 1995)
19	Fodder radish (*Raphanus sativus* L.)	8	1-Sep-93	14-Mar-94	195	1229	Catch crop; effect of large water supply	normal water supply	(Van Dam and Leffelaar, 1998)
11	Leek (*Allium porrum* L.)	13	12-Jun-92	9-Nov-92	151	2189	Nitrogen level and drought	200 kg N; optimal water supply	(Smit et al., 1995; Smit et al., 1996; Smit and Zuin, 1996)
11	Leek (*Allium porrum* L.)	9	12-Jun-92	9-Nov-92	151	2189	Nitrogen level and drought	100 kg N; optimal water supply	(Smit et al., 1995; Smit et al., 1996; Smit and Zuin, 1996)
7	Leek (*Allium porrum* L.)	14	17-Jun-91	26-Nov-91	183	2415	Nitrogen level	125 kg N short period with no water	(Smit et al., 1995; Smit et al., 1996; Smit and Zuin, 1996)
7	Leek (*Allium porrum* L.)	16	17-Jun-91	26-Nov-91	183	2415	Nitrogen level	250 kg N short period with no water	(Smit et al., 1995; Smit et al., 1996; Smit and Zuin, 1996)
32	Lupins (*Lupinus albus*)	1	18-Jun-98	6-Nov-98	142	1982	Phytoremediation of PACs; drought	Anthracene and pyrene (but no effect on growth) profile 50 cm	
32	Lupins (*Lupinus albus*)	5	18-Jun-98	6-Nov-98	142	1982	Phytoremediation of PACs; drought	No addition of PAC's; optimal water supply	

Table 2. Continued

Experi- ment #	Crop	Compart- ment #	Date of planting	End date	No. of days	Thermal time at the end of exp.	Experimental factors varied in the experiment	Treatment in control compartments	References/comments
12	Maize (*Zea mays* L.)	16	15-Apr-92	22-Jun-92	69	975	Nitrogen application (placement) experiment	50 kg N; broadcast	(Schröder et al., 1994; Schröder et al., 1996)
13	Maize (*Zea mays* L.)	14	3-Jul-92	31-Aug-92	60	1073	Nitrogen application (placement) experiment	50 kg N; broadcast	(Schröder et al., 1994; Schröder et al., 1996)
16	Maize (*Zea mays* L.)	16	15-Apr-93	14-Jun-93	61	895	Nitrogen application (placement) experiment	50 kg N; broadcast	(Schröder et al., 1994; Schröder et al., 1996)
17	Maize (*Zea mays* L.)	12	1-Jul-93	31-Aug-93	62	954	Nitrogen application (placement) experiment	50 kg N; broadcast	(Schröder et al., 1994; Schröder et al., 1996)
6	Potato[a] (*Solanum tuberosum* L.)	4	17-May-91	40-Oct-91	166	2391	Potato cyst nematodes (*Globodera pallida*)	No nematodes	(Haverkort et al., 1994; Smit and Vamerali, 1998)
10	Potato (*Solanum tuberosum* L.)	4	28-Apr-92	15-Sep-92	141	2319	Drought; potato cyst nematodes (*Globodera pallida*)	No nematodes, optimal water supply	(Haverkort et al., 1994; Smit and Vamerali, 1998)
15	Potato (*Solanum tuberosum* L.)	4	6-May-93	16-Aug-93	103	1606	Nitrogen; Variety	Variety Bintje; 200 kg N/ha	
15	Potato (*Solanum tuberosum* L.)	6	6-May-93	16-Aug-93	103	1606	Nitrogen; Variety	Variety Gloria; 200 kg N/ha	
21	Potato (*Solanum tuberosum* L.)	2	11-May-94	28-Sep-94	139	2260	Sterilisation (gamma irradiation), Potato cyst nematodes; pH	pH 4.9; upper 30 cm profile sterilized	
21	Potato (*Solanum tuberosum* L.)	6	11-May-94	28-Sep-94	139	2260	Sterilisation (gamma irradiation, Potato cyst nematodes; pH	pH 6.0; upper 30 cm profile sterilized	
25	Potato (*Solanum tuberosum* L.)	2	12-May-95	21-Aug-95	102	1701	Potato cyst nematodes, pH	pH 4.6; no nematodes upper 30 cm profile sterilised	(De Ruijter and Haverkort, 1999)

Table 2. Continued

Experiment #	Crop	Compartment #	Date of planting	End date	No. of days	Thermal time at the end of exp.	Experimental factors varied in the experiment	Treatment in control compartments	References/comments
25	Potato (*Solanum tuberosum* L.)	6	13-May-95	21-Aug-95	102	1701	Potato cyst nematodes, pH	pH 6.0; no nematodes upper 30 cm profile sterilised	(De Ruijter and Haverkort, 1999)
27	Potato (*Solanum tuberosum* L.)	1	15-May-96	10-Sep-96	118	1790	Split applications of nitrogen, drought	60 kg N at planting; 140 kg N in June, optimal water supply	(Vos et al., 1999)
27	Potato (*Solanum tuberosum* L.)	2	15-May-96	10-Sep-96	118	1790	Split applications of nitrogen, drought	200 kg N at planting; optimal water supply	
27	Potato (*Solanum tuberosum* L.)	5	15-May-96	10-Sep-96	118	1790	Split applications of nitrogen, drought	200 kg N at planting; optimal water supply crop in growth chamber	(Vos et al., 1999)
27	Potato (*Solanum tuberosum* L.)	8	15-May-96	10-Sep-96	118	1790	Split applications of nitrogen, drought	60 kg N at planting; 140 kg N in June, optimal water supply	(Vos et al., 1999)
22a	Beetroot (*Beta vulgaris* L.)	10,12,14,16	27-May-94	2-Aug-94	68	1181	crop after spinach (exp. 22)	no nitrogen no treatment	
24a	Beetroot (*Beta vulgaris* L.)	10,12,14,16	2-Jun-95	8-Oct-95	129	2169	crop after spinach (exp. 24)	50 kg nitrogen at planting	
20	Ryegrass (*Lolium perenne*)	1	11-Oct-93	9-Jun-94	242	1574	CO_2 level	350 ppm CO_2 crop in growth chamber	(Schapendonk et al., 1996; Schapendonk et al., 1997)
20	Ry grass (*Lolium perenne*)	5	11-Oct-93	9-Jun-94	242	1574	CO_2 level	350 ppm CO_2 crop in growth chamber	(Schapendonk et al., 1996; Schapendonk et al., 1997)
22	Spinach (*Spinacia oleracea* L.)	10	30-Mar-94	17-May-94	49	487	Nitrogen location	60 kg N in 0–10 cm layer	
22	Spinach (*Spinacia oleracea* L.)	16	30-Mar-94	17-May-94	49	487	Nitrogen location	120 kg N in 0–10 cm layer	
24	Spinach (*Spinacia oleracea* L.)	12	7-Apr-95	19-May-95	42	405	Nitrogen location	60 kg N in 0–10 cm layer	
24	Spinach (*Spinacia oleracea* L.)	14	7-Apr-95	19-May-95	42	405	Nitrogen location	120 kg N in 0–10 cm layer	
5	Spring wheat (*Triticum aestivum* L.)	3	4-Apr-91	26-Aug-91	145	1909	CO_2 level	350 ppm CO_2 crop in growth chamber	(Dijkstra et al., 1996; Geijn et al., 1993; Grashoff et al., 1995)

Table 2. Continued

Experiment #	Crop	Compartment #	Date of planting	End date	No. of days	Thermal time at the end of exp.	Experimental factors varied in the experiment	Treatment in control compartments	References/comments
5	Spring wheat (*Triticum aestivum* L.)	7	4-Apr-91	26-Aug-91	145	1909	CO_2 level	350 ppm CO_2 crop in growth chamber	(Dijkstra et al., 1996; Geijn et al., 1993; Grashoff et al., 1995)
23	Winter rye (*Secale cereale* L)	10	24-Aug-94	13-Mar-95	202	1659	Catch crop; Nitrogen level and location	70 kg N in 0–10 cm layer	(Van Dam and Leffelaar, 1998)
23	Winter rye (*Secale cereale* L)	14	24-Aug-94	13-Mar-95	202	1659	Catch crop; Nitrogen level and location	70 kg N at depth of 40–50 cm	(Van Dam and Leffelaar, 1998)
23	Winter rye (*Secale cereale* L)	16	24-Aug-94	13-Mar-95	202	1659	Catch crop; Nitrogen level and location	70 kg N at depth of 40–50 cm	(Van Dam and Leffelaar, 1998)
14	Winter wheat (*Triticum aestivum* L.)	1	19-Nov-92	11-Aug-93	266	2533	CO_2 level	350 ppm CO_2 crop in growth chamber	(Dijkstra et al., 1999)
14	Winter wheat (*Triticum aestivum* L.)	5	19-Nov-92	11-Aug-93	266	2533	CO_2 level	350 ppm CO_2 crop in growth chamber	(Dijkstra et al., 1999)

[a]In all the potato experiments rooted eye cuttings, not tubers, were planted.

Using the regression coefficients for root number vs. thermal time we calculated $T_{r,z,0}$ and $T_{r,z,0.5}$ for each depth–compartment combination, averaged over compartments and calculated the standard deviation. The latter reflects the variation between compartments (replicates) and is indicated in Table 3 and Figures 3 and 4. The goodness of fit of the linear regression procedure is reflected in the coefficient of determination (r^2), also averaged for each crop–depth combination.

Results and discusssion

As an example, root data from one of the compartments of experiment 5 are presented in Figure 1. This experiment investigated the effect of higher ambient CO_2 concentrations in the atmosphere (see Table 2 for more details). For four depths, $N_{r,z}$ has been plotted against time (Figure 1a) and against thermal time (Figure 1b). Figure 1b shows that for all depths the increase in root number was linear at least until a value of 0.7 cm^{-2}.

Figure 2 then visualizes the regression procedure for four selected depths in this compartment. For each depth in each compartment the regression equation yielded a slope ($=\Delta N_{r,z,l}$) and intercept with the y-axis. The average of the coefficients for the available compartments is presented in columns 4 and 5 of Table 3, together with the average coefficient of determination (r^2, column 6).

Table 3 also shows the time the first roots arrived at each depth, in days after planting (DAP, column 7); thermal time and time in DAP at maximum root number at that depth (columns 8 and 9, respectively) and the maximum root number (column 10). In the following paragraphs the differences between crops for these rooting characteristics will be presented and discussed.

Maximum root number

There are large differences in maximum root number between crops: common velvet grass shows extremely high maximum root numbers in the upper soil layers (up to 30 cm^{-2}), but even at

Table 3. Summary of the results, per depth, of the regression procedure for the linear phase of root #/cm^{-2} vs. thermal time after planting (column 4 (intercept); column 5 (slope); column 6 (the coefficient of determination)). Column 7 shows for each depth the date the first roots were observed (in DAP). The thermal time at which the maximum root number (in column 10) was observed is shown in column 8, the corresponding number of days (DAP) in column 9. Values are averages for the number of compartments (column 3). In columns 7–10 the standard deviations are shown in brackets

1 Crop	2 Depth (cm)	3 No. of compartments	4 Average intercept (cm^{-2})	5 Average slope ($\Delta N_{r,z,l}$) (°C day)$^{-1}$	6 Average r^2 (%)	7 First roots observed (DAP)	8 Average thermal time at max. root #	9 DAP at maximum root #	10 Max. Root # ($N_{r,z,m}$)(cm^{-2})
Alfalfa	5	1	−0.30	0.00511	96	16 (–)	889 (–)	58 (–)	3.3 (–)
	20	1	−0.35	0.00158	98	31 (–)	889 (–)	58 (–)	1.0 (–)
	45	1	−0.48	0.00116	94	45 (–)	1789 (–)	114 (–)	0.6 (–)
	60	1	−0.45	0.00073	97	58 (–)	1789 (–)	114 (–)	0.8 (–)
	80	1	−0.46	0.00073	98	58 (–)	2517 (–)	170 (–)	0.6 (–)
	100	1	−0.33	0.00041	97	72 (–)	2711 (–)	192 (–)	0.4 (–)
	125	1	−0.64	0.00052	95	85 (–)	2711 (–)	192 (–)	0.3 (–)
	150	1	−0.74	0.00060	99	85 (–)	2517 (–)	170 (–)	0.8 (–)
Brussels sprouts	5	2	−0.73	0.00356	97	8 (0)	1937 (460)	127 (39)	5.8 (0.4)
	10	2	−0.36	0.00125	96	15 (0)	2316 (77)	162 (11)	1.9 (0.0)
	15	2	−0.38	0.00118	94	23 (0)	2316 (77)	162 (11)	2.1 (0.6)
	20	2	−0.24	0.00097	97	23 (0)	2339 (109)	169 (21)	1.6 (0.3)
	30	2	−0.27	0.00096	96	29 (0)	2371 (0)	169 (0)	1.1 (0.2)
	45	2	−0.60	0.00151	94	29 (0)	2316 (77)	162 (11)	1.3 (0.2)
	60	2	−0.49	0.00093	97	43 (0)	2204 (299)	155 (40)	1.1 (0.2)
	80	2	−1.00	0.00128	96	64 (11)	2204 (299)	155 (40)	1.1 (0.3)
	100	2	−2.50	0.00320	97	56 (0)	2109 (433)	148 (49)	2.4 (0.6)
Common velvet grass	5	1	−4.95	0.02567	94	15 (–)	1655 (–)	105 (–)	29.7 (–)
	10	1	−2.78	0.01093	96	15 (–)	1254 (–)	78 (–)	10.2 (–)
	15	1	−7.05	0.01801	92	35 (–)	1254 (–)	78 (–)	14.4 (–)
	20	1	−7.59	0.01538	97	35 (–)	1456 (–)	92 (–)	14.2 (–)
	30	1	−2.37	0.00358	95	55 (–)	1655 (–)	105 (–)	3.6 (–)
	45	1	−1.71	0.00257	91	55 (–)	1655 (–)	105 (–)	2.5 (–)
	60	1	−7.88	0.00807	92	78 (–)	1655 (–)	105 (–)	5.8 (–)
Field bean	5	2	−0.18	0.00061	97	36 (0)	1599 (1155)	111 (67)	0.3 (0.2)
	10	2	−0.30	0.00127	97	29 (10)	1018 (334)	77 (20)	0.8 (0.0)
	15	2	−0.17	0.00074	91	43 (9)	1131 (175)	84 (10)	0.6 (0.1)
	20	2	−0.18	0.00056	99	43 (9)	1254 (0)	91 (0)	0.3 (0.2)
	30	2	−0.15	0.00033	98	56 (10)	1639 (544)	112 (30)	0.2 (0.1)
	45	2	−0.09	0.00019	95	70 (10)	1375 (171)	98 (10)	0.1 (0.1)

Table 3. Continued

1 Crop	2 Depth (cm)	3 No. of compartments	4 Average intercept (cm^{-2})	5 Average slope ($\Delta N_{r,z,l}$) (°C day)$^{-1}$	6 Average r^2 (%)	7 First roots observed (DAP)	8 Average thermal time at max. root #	9 DAP at maximum root #	10 Max. Root # ($N_{r,z,m}$)(cm^{-2})
	60	2	−0.14	0.00024	99	63 (0)	1375 (171)	98 (10)	0.2 (0.0)
	80	2	−0.26	0.00034	97	77 (0)	1375 (171)	98 (10)	0.2 (0.1)
	100	2	−0.16	0.00020	96	77 (0)	1544 (410)	107 (23)	0.1 (0.0)
Fodder radish	5	1	−0.05	0.00061	95	9 (−)	1030 (−)	147 (−)	0.9 (−)
	10	1	−0.14	0.00124	96	9 (−)	1030 (−)	147 (−)	0.5 (−)
	15	1	−0.08	0.00064	95	9 (−)	1105 (−)	177 (−)	0.7 (−)
	20	1	−0.12	0.00096	96	9 (−)	1105 (−)	177 (−)	1.0 (−)
	30	1	−0.13	0.00079	93	23 (−)	1030 (−)	147 (−)	0.4 (−)
	45	1	−0.22	0.00077	94	23 (−)	1105 (−)	177 (−)	0.6 (−)
	60	1	−0.21	0.00089	99	23 (−)	1030 (−)	147 (−)	0.5 (−)
	80	1	−0.69	0.00167	95	36 (−)	1030 (−)	147 (−)	0.8 (−)
	100	1	−1.32	0.00337	86	36 (−)	1030 (−)	147 (−)	1.7 (−)
Leeks	5	4	−0.55	0.00084	90	37 (9)	1956 (447)	132 (38)	1.2 (0.9)
	10	4	−0.25	0.00053	94	34 (14)	1946 (212)	125 (24)	0.7 (0.3)
	15	4	−0.21	0.00075	95	20 (6)	2141 (89)	148 (16)	1.2 (0.4)
	20	4	−0.07	0.00054	98	16 (8)	1941 (338)	127 (32)	0.8 (0.4)
	30	4	−0.07	0.00035	95	23 (6)	1962 (247)	128 (22)	0.5 (0.2)
	45	4	−0.26	0.00047	98	37 (12)	2031 (61)	131 (8)	0.7 (0.1)
	60	4	−0.15	0.00026	92	41 (11)	2076 (96)	138 (11)	0.4 (0.4)
	80	2	−0.18	0.00020	90	54 (0)	2205 (0)	165 (0)	0.3 (0.0)
Lupins	5	2	−0.20	0.00197	93	15 (0)	1157 (137)	71 (10)	2.2 (0.6)
	10	2	−0.45	0.00170	99	15 (0)	1060 (0)	64 (0)	1.7 (0.4)
	15	2	−0.27	0.00090	89	15 (0)	1254 (0)	78 (0)	1.4 (0.2)
	20	2	−0.25	0.00073	90	19 (5)	985 (106)	60 (6)	0.6 (0.6)
	30	2	−0.15	0.00054	100	22 (0)	1555 (140)	99 (9)	0.4 (0.2)
	45	2	−0.15	0.00043	92	35 (0)	1555 (140)	99 (9)	0.5 (0.2)
	60	2	−0.32	0.00087	100	35 (0)	1456 (1456)	92 (0)	0.7 (0.3)
Maize	5	4	−0.97	0.00442	97	20 (11)	864 (157)	57 (15)	2.3 (1.5)
	10	3	−0.35	0.00195	97	22 (13)	1000 (64)	64 (5)	1.6 (1.2)
	15	3	−0.63	0.00276	95	22 (13)	1000 (64)	64 (5)	2.1 (2.3)
	20	3	−0.69	0.00182	94	29 (12)	1000 (64)	64 (5)	1.2 (0.9)
	30	4	−0.72	0.00178	92	34 (9)	974 (74)	63 (4)	1.1 (0.8)

Table 3. Continued

1 Crop	2 Depth (cm)	3 No. of compartments	4 Average intercept (cm^{-2})	5 Average slope ($\Delta N_{r,z,l}$) (°C day)$^{-1}$	6 Average r^2 (%)	7 First roots observed (DAP)	8 Average thermal time at max. root #	9 DAP at maximum root #	10 Max. Root # ($N_{r,z,m}$)(cm^{-2})
	45	4	−0.78	0.00137	94	46 (13)	974 (74)	63 (4)	0.6 (0.4)
	60	4	−0.66	0.00100	98	53 (6)	974 (74)	63 (4)	0.4 (0.2)
Potato	5	12	−1.05	0.00870	94	11 (5)	854 (605)	57 (37)	2.8 (1.1)
	10	12	−1.15	0.00991	96	13 (4)	587 (421)	40 (23)	2.4 (1.1)
	15	12	−0.73	0.00512	93	21 (4)	860 (640)	56 (36)	1.9 (0.7)
	20	12	−1.26	0.00628	94	24 (5)	769 (388)	52 (22)	2.0 (0.9)
	30	12	−1.81	0.00639	94	29 (10)	905 (592)	59 (34)	1.8 (0.5)
	45	12	−0.91	0.00225	96	38 (8)	1069 (450)	71 (26)	1.0 (0.4)
	60	12	−0.82	0.00162	94	50 (11)	1228 (410)	80 (23)	0.9 (0.3)
	80	11	−0.96	0.00135	94	63 (12)	1543 (446)	98 (24)	0.7 (0.4)
	100	9	−0.92	0.00087	94	82 (17)	1784 (300)	113 (17)	0.5 (0.3)
Beetroot	5	8	−0.44	0.00220	94	16 (3)	1053 (404)	63 (21)	1.4 (0.6)
	10	8	−0.44	0.00183	95	27 (9)	886 (343)	54 (17)	0.7 (0.2)
	15	8	−0.41	0.00139	94	33 (8)	924 (256)	56 (13)	0.7 (0.1)
	20	8	−0.53	0.00149	95	33 (8)	1026 (287)	61 (15)	0.9 (0.3)
	30	8	−0.49	0.00132	97	36 (5)	994 (217)	59 (11)	0.7 (0.3)
	45	8	−0.57	0.00120	96	43 (9)	1034 (142)	61 (7)	0.7 (0.1)
	60	8	−0.99	0.00179	92	53 (8)	1139 (128)	66 (6)	1.0 (0.3)
Ryegrass	5	2	−2.13	0.00629	88	39 (0)	1408 (0)	228 (0)	4.6 (0.7)
	10	2	−1.99	0.00456	97	88 (0)	1269 (431)	218 (35)	2.2 (0.1)
	15	2	−2.29	0.00456	96	108 (0)	1038 (234)	196 (24)	1.9 (0.3)
	20	2	−2.51	0.00449	99	123 (0)	1204 (0)	213 (0)	1.7 (0.2)
	30	2	−1.60	0.00243	96	151 (0)	1306 (144)	221 (11)	1.4 (0.2)
	45	2	−1.39	0.00192	94	165 (0)	1408 (0)	228 (0)	1.2 (0.0)
	60	2	−1.39	0.00146	98	196 (24)	1574 (0)	242 (0)	0.9 (0.2)
	80	2	−1.15	0.00101	98	213 (0)	1574 (0)	242 (0)	0.4 (0.1)
Spinach	5	4	−0.60	0.00568	94	16 (1)	431 (69)	44 (7)	1.6 (0.6)
	10	4	−0.52	0.00417	96	20 (3)	423 (43)	44 (3)	1.2 (0.2)
	15	4	−0.75	0.00462	96	22 (2)	446 (47)	46 (4)	1.3 (0.4)
	20	4	−0.77	0.00400	93	27 (3)	423 (43)	44 (3)	1.0 (0.4)
	30	4	−1.00	0.00384	88	29 (1)	446 (47)	46 (4)	0.7 (0.1)
	45	4	−0.69	0.00207	95	39 (4)	446 (47)	46 (4)	0.2 (0.2)
	60	3	−0.90	0.00244	100	43 (1)	459 (47)	47 (4)	0.2 (0.2)

Table 3. Continued

1 Crop	2 Depth (cm)	3 No. of compartments	4 Average intercept (cm^{-2})	5 Average slope ($\Delta N_{r,z,l}$) ($(°C\ day)^{-1}$)	6 Average r^2 (%)	7 First roots observed (DAP)	8 Average thermal time at max. root #	9 DAP at maximum root #	10 Max. Root # ($N_{r,z,m}$)(cm^{-2})
Spring wheat	5	2	−0.83	0.00688	99	15 (0)	477 (93)	57 (9)	2.0 (0.1)
	10	2	−0.50	0.00388	99	15 (0)	411 (0)	50 (0)	1.1 (0.1)
	15	2	−0.32	0.00263	99	15 (0)	411 (0)	50 (0)	0.8 (0.1)
	20	2	−0.30	0.00232	100	15 (0)	637 (134)	71 (11)	1.0 (0.6)
	30	2	−0.40	0.00259	96	22 (0)	1222 (0)	106 (0)	1.4 (1.0)
	45	2	−0.64	0.00265	96	36 (0)	1222 (0)	106 (0)	1.2 (0.6)
	60	2	−0.77	0.00307	99	36 (0)	1468 (0)	120 (0)	2.0 (0.3)
	80	2	−0.91	0.00244	99	50 (0)	1468 (0)	120 (0)	2.7 (1.1)
	100	2	−0.35	0.00085	99	63 (0)	1816 (132)	140 (8)	1.3 (0.6)
Winter rye	5	3	−0.01	0.00170	96	9 (0)	1476 (165)	172 (27)	0.9 (0.1)
	10	3	0.01	0.00338	93	9 (0)	1620 (34)	195 (6)	0.6 (0.1)
	15	3	−0.07	0.00088	94	9 (0)	1620 (34)	195 (6)	0.5 (0.1)
	20	3	−0.08	0.00093	96	9 (0)	1278 (544)	143 (82)	0.5 (0.1)
	30	3	−0.17	0.00096	86	18 (4)	1278 (544)	143 (82)	0.5 (0.1)
	45	3	−0.33	0.00138	92	23 (0)	841 (435)	79 (61)	0.5 (0.0)
	60	3	−0.52	0.00135	96	28 (4)	1050 (342)	97 (41)	0.4 (0.1)
	80	3	−0.42	0.00107	84	32 (4)	883 (395)	83 (57)	0.3 (0.1)
	100	3	−0.90	0.00183	93	37 (0)	1487 (99)	173 (16)	0.9 (0.3)
Winter wheat	5	2	−0.05	0.00102	98	22 (0)	1322 (0)	189 (0)	4.0 (0.6)
	10	2	−0.08	0.00087	94	22 (0)	1322 (0)	189 (0)	3.3 (0.6)
	15	2	−0.11	0.00075	94	22 (0)	1224 (139)	183 (9)	2.0 (0.1)
	20	2	−0.10	0.00058	90	29 (9)	1224 (139)	183 (9)	1.7 (0.2)
	30	2	−0.15	0.00062	90	43 (11)	1224 (139)	183 (9)	1.7 (0.3)
	45	2	−0.73	0.00180	95	71 (11)	1126 (0)	176 (0)	1.3 (0.1)
	60	2	−0.70	0.00182	97	93 (0)	1224 (139)	183 (9)	1.4 (0.2)
	80	2	−1.04	0.00233	99	106 (0)	1224 (139)	183 (9)	1.8 (0.1)
	100	2	−1.55	0.00330	98	106 (0)	1224 (139)	183 (9)	2.4 (0.4)

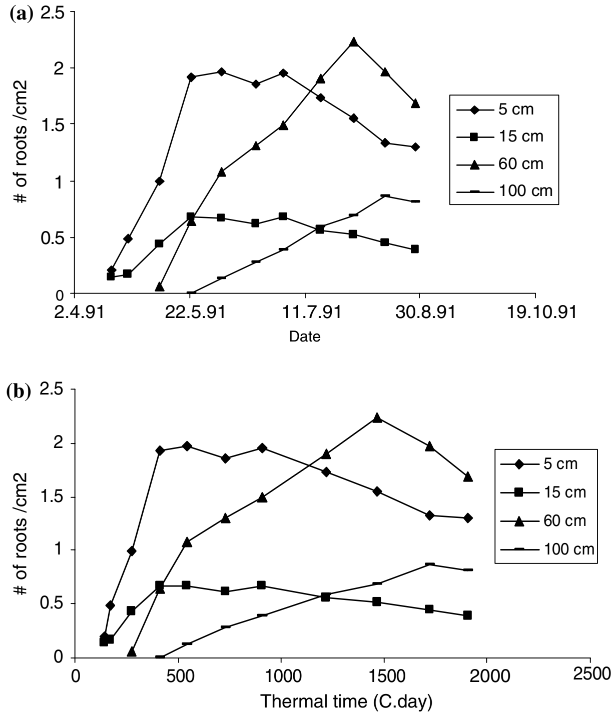

Figure 1. The number of roots per cm^2 at 5, 15, 80 and 100 cm depths for the control compartment of experiment 5 (spring wheat, see Table 2) as function of time (a) and thermal time (b).

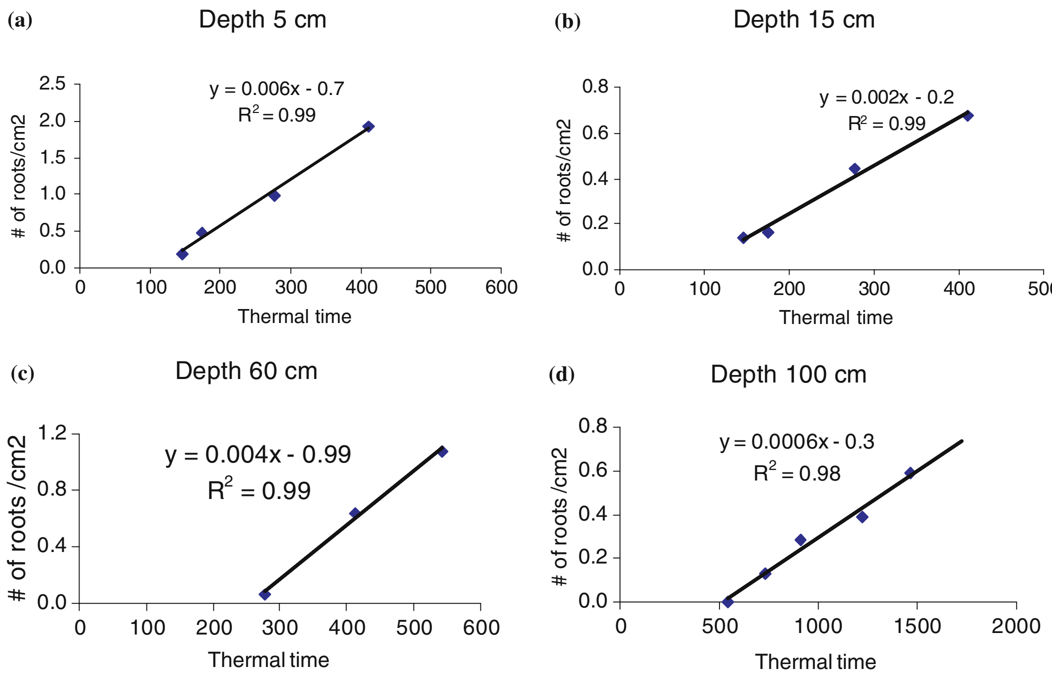

Figure 2. The number of roots per cm^2 minirhizotron surface as function of thermal time (restricted to the linear phase of development) for spring wheat at 4 depths: 5 cm (a), 15 cm (b), 60 cm (c) and 100 cm (d).

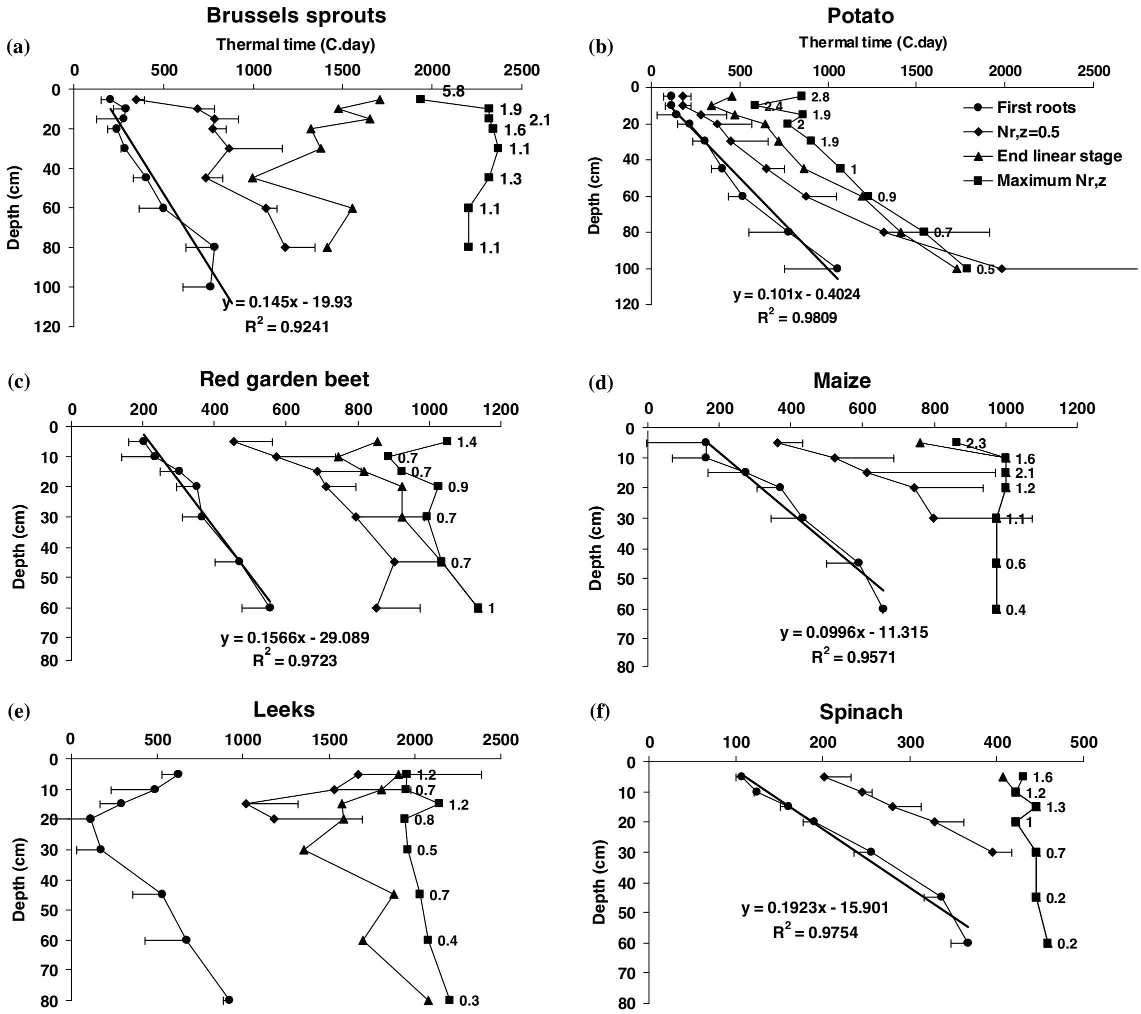

Figure 3. Thermal time after planting at 'first roots visible' ($N_{r,z,0}$, ●), at root number = 0.5 cm^{-2}($N_{r,z,0.5}$, ◆), at end of linear phase of root number increase ($N_{r,z,el}$, ▲) and at maximum root number observed ($N_{r,z,m}$, ■) vs. depth for Brussels sprouts (a), potatoes (b), red garden beet (c), maize (d), leeks (e) and spinach (f). The maximum root number has been indicated (in cm^{-2}).

a depth of 60 cm rooting is very intensive compared to crops like field bean, leeks and fodder radish. Brussels sprouts show large root numbers in the top 10 cm of the profile and a very homogeneous rooting in the rest of the profile to a depth of 100 cm. Potatoes ultimately developed intensive rooting in the upper part of the profile (until 40 cm) but at greater depths rooting was less than 1 root cm^{-2}.

Rooting depth and root proliferation rate

As the maximum root number at each depth does not give much information on the dynamics of rooting (i.e. how fast a crop can explore the soil profile) we have plotted the thermal time associated with $N_{r,z,0}$ and $N_{r,z,0.5}$ against depth for most crops (Figures 3 and 4). In these two Figures the thermal time at the end of the linear stage of root number increase ($N_{r,z,el}$) and at maximum root number $N_{r,z,m}$. are also indicated.

Figure 3a (Brussels sprouts) shows that not until approximately 500 °C day do the first roots arrive at a depth of 60 cm; the first roots reach 100 cm after 800 °C day. For nearly all crops the relationship of $T_{r,z,0}$ with depth was linear (the regression equation is indicated in the graph).

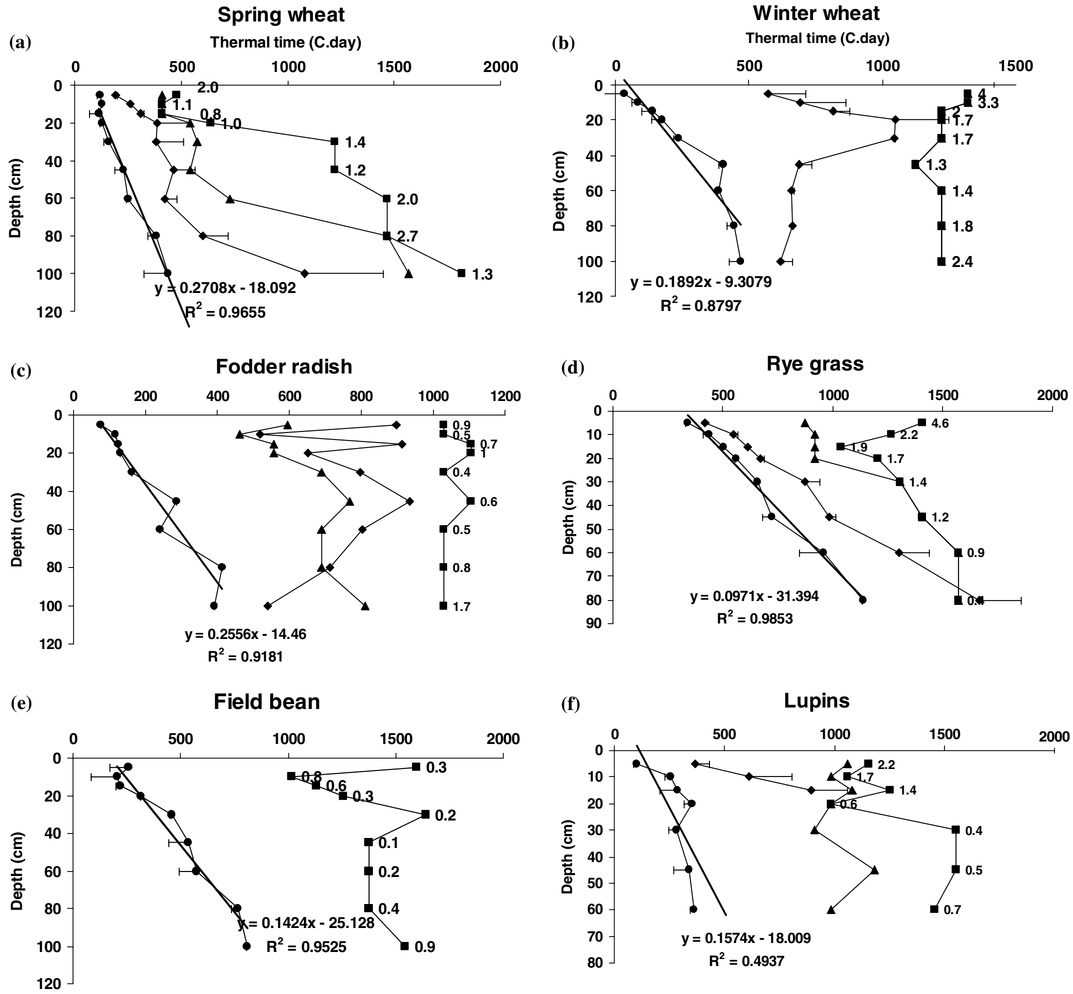

Figure 4. Thermal time after planting at 'first roots visible' ($N_{r,z,0}$, ●), at root number = 0.5 cm^{-2}($N_{r,z,0.5}$, ◆), at end of linear phase of root number increase ($N_{r,z,el}$, ▲) and at maximum root number observed ($N_{r,z,m}$, ■) vs. depth for spring wheat (a), winter wheat (b), fodder radish (c), ryegrass (d), field bean (e) and lupins (f). The maximum root number has been indicated (in cm^{-2}).

The rate at which the number of roots increases after their first appearance at a certain depth can be deduced by comparing the line of $T_{r,z,0}$ (first roots) with the line of $T_{r,z,0.5}$ (root # = 0.5 cm^{-2}). The smaller the horizontal distance between the two lines in thermal time, the faster the proliferation rate. For a Brussels sprouts crop it takes approximately 400–500 °C day at all depths for $N_{r,z}$ to go from 0 to 0.5 cm^{-2}. Usually, rooting decreases exponentially with depth. However, in Brussels sprouts we observed a larger root number and a faster proliferation at a depth of 100 cm than at shallower depths. This turned out to be an experimental artifact caused by the abrupt change at 100 cm in most Rhizolab experiments from a humic sandy soil to a coarse non-humic sand. At the end of the experiments it was observed that no roots had penetrated this subsoil (probably because of its much lower water content). At the boundary between the two soil types the roots proliferated (in effect, they were deflected) resulting in a higher maximum root number and proliferation here than at shallower depths. For Brussels sprouts therefore, the increase in root number at 100 cm has not been indicated in Figure 3a.

For a potato crop the graph (B) shows that increase in root number takes much less thermal time in the upper part of the profile (100 °C day for root numbers to go from 0 to 0.5 cm^{-2}) than deeper in the profile (almost 700 °C day). The graph for potato also shows that the roots do not reach a depth of 100 cm until after 1000 °C day, whereas the roots of a Brussels sprouts crop had already arrived at this depth after 700 °C days after planting.

Red garden beet (Figure 3c) needs 200 °C day before the first roots are observed at a depth of 5 cm and another 200 °C.day to go from 0 to 0.5 cm^{-2}; at a depth of 45 cm the figures are 450 °C day (first roots) and 450 °C day (0.5 cm^{-2}). Maize behaves similarly (Figure 3d). In the graph for maize $T_{r,z,0.5}$ is not shown below 35 cm because the experiments were too short to obtain sufficient rooting at these depths.

Leeks (Figure 3e) show a different rooting pattern: at 20–30 cm depth the first roots appeared rapidly, but above and below this depth they appeared much later. We attribute this to the planting depth being around 15 cm, which was therefore the depth at which the roots were initiated. Geotropism does not seem to have a large influence on this crop, as the soil above this depth is explored in an identical way to the deeper soil. Leeks explore the depth slowly (it takes 1000 °C day before the first roots arrive at a depth of 80 cm and, moreover, the increase in root number is very slow: at all depths it takes another 1000 °C day before a root number of 0.5 is achieved). In the case of leeks, the shallow rooting characteristic in combination with low uptake rates is especially pertinent to the loss of nitrogen by leaching (Smit et al., 1996).

The rooting characteristics of leeks contrast with those of spinach (Figure 3f) which shows a relatively fast exploration of the profile: the first roots arrive at a depth of 60 cm after only 350 °C day. Down to a depth of 30 cm the root number increases fast (only 100–150 °C day from 0 to 0.5 cm^{-2}); the short growing period of the crop prevents rooting from intensifying deeper in the profile. The main reason nitrogen leaching occurs when this crop is grown is that it is harvested in full growth, at the time that the crop needs a large amount of nitrogen in the vicinity of the roots. On the other hand, sometimes the quality of the root system has been indicated as a factor preventing a crop from using nitrogen efficiently. Schenk et al. (1991) concluded that in the case of spinach, about 80% of total root length was in the top 15 cm of soil and less than 5% was below 30 cm; they also observed that spinach roots were only present from 15 to 30 cm depth during the last 2 weeks before harvest. This is in agreement with the data from our experiments (Table 2, Table 3 and Figure 3f). Although the roots of this crop grow down fast and increase in number is faster than other crops (around 100–150 °C day to go from 0 to 0.5 cm^{-2} in the top 30 cm), the main problem when growing a spinach crop is that the growing period is so short that sufficient roots cannot be formed deeper in the soil. For this reason, spinach does not qualify as an inherent shallow-rooting crop. Nevertheless, for the purpose of fertiliser recommendations it should be treated as a shallow-rooting crop and the fertiliser rate must be based on the mineral N content of the upper soil layers. By contrast, in crops like Brussels sprouts the nitrogen leached to deeper soil layers is not lost *per se*.

The cereals (spring wheat, winter wheat (Figure 4a, b) and winter rye (not shown) are characterised by fast downward rooting; it takes 500 °C day for the first roots to appear at a depth of 100 cm. When the first roots appear at this depth, root number in the upper 60 cm of the profile already exceeds 0.5 cm^{-2}. Winter wheat needs more thermal time, at least according to our data, especially for the 20–40 cm layer.

Fodder radish (Figure 4c) roots grow down even faster (only 400 °C day to arrive at 100 cm depth) but, in contrast, the increase in root number is slow: at each depth the calculated $T_{r,z,0.5}$ was beyond the end of the linear phase. As already indicated, such an extrapolation probably leads to an underestimation of the thermal time needed.

Ryegrass (Figure 4d) roots grow downwards much slower after sowing, but root number increases fast, especially in the upper 30 cm of the soil profile.

Compared to the other crops we found field beans to have very low root numbers (Figure 4e), therefore we did not calculate $N_{r,z,0.5}$. Field beans have been reported to have a low root length density, which Kage (1997) suggests could be the reason for a high residual nitrate content in the soil profile after the crop has been harvested. At a depth of 40 cm he measured a volumetric root length density of only

0.05–0.10 cm^{-2}. At this depth under the optimal conditions of the Rhizolab the root number was 0.1–0.2 cm^{-2}, which might correspond to a root length density of 0.2–0.4 cm^{-2}. Though low, these values are higher than those Kage (1997) reported.

Root front velocity

Figures 3 and 4 demonstrate that crops differ widely in the downward rate of rooting and in root proliferation. The Figures also show that a fast downward exploration of the profile does not always coincide with a fast increase in root numbers, implying that these two rooting characteristics are more or less independent of each other. Focusing on the root front velocity, the graphs show that with the exception of leeks, in all crops a simple linear regression can describe the relationship between $T_{r,z,0}$ and depth. Table 4 summarises the results of this regression, for all crops. The leek data for depths of 5, 10 and 25 cm were excluded, for the reasons mentioned above. The slope of the regression coefficient now gives the downward rate of the root in cm per °C day. The crops with slow downward rates include leeks, ryegrass and common velvet grass (despite the latter's abundant rooting), maize and potato. Fast rates are found for the cereal crops, fodder radish and also spinach. In Table 4 it is also indicated what the downward velocity of the root front would be in a day with an average temperature of 15 °C and in a day with an average temperature of 20 °C. For most crops the rate at 15 °C is between 1.5 and 2.5 cm per day.

Bland (1993) reports downward rates of root growth of between 0.7 and 1.7 cm day^{-1} for cotton and between 0.9 and 2.6 cm day^{-1} for soybean, with the values depending on temperature. Stone et al., (2001) give some data for sorghum and sunflower: from 20–60 days after emergence the rooting front depth increased by 2.5 cm day^{-1} in sorghum and 4.1 cm day^{-1} in sunflower. The corresponding figures from 60 to 90 days rooting were much lower: only 0.8 and 0.6 cm day^{-1}, respectively. For winter cereals a better comparison with our results can be made, as Barraclough and Leigh (1984) report a linear relationship between accumulated thermal time and rooting depth. They calculated a slope of 0.179 cm per °C day. This corresponds with the values of 0.176 and 0.189 we found for winter rye and winter wheat. Masse et al. (1991) reported a rate of only 0.12 for winter wheat.

For fodder radish Thorup Kristensen (1993b) reported very high root front rates

Table 4. The relationship between depth (cm) and thermal time (°C day) and $N_{r,z,0}$ (first roots). Based on the slope of the regression (in cm (°C day)$^{-1}$) the "velocity of the root front" was calculated for average temperatures of 15 °C and 20 °C

Crop	Regression coefficients			Estimated 'root front' velocity in cm day^{-1} at	
	Intercept	Slope	r^2 (%)	15 °C	20 °C
Alfalfa	−5.6	0.125	96.3	1.9	2.5
Brussels sprouts	−19.9	0.145	92.4	2.2	2.9
Common velvet grass	−10.5	0.071	93.9	1.1	1.4
Field bean	−25.1	0.142	95.3	2.1	2.8
Fodder radish	−14.5	0.256	91.8	3.8	5.1
Leeks[a]	13.5	0.070	97.5	1.0	1.4
Lupins	−18.0	0.157	49.4	2.4	3.1
Maize	−11.3	0.100	95.7	1.5	2.0
Potato	−0.4	0.101	98.1	1.5	2.0
Beetroot	−29.1	0.157	97.2	2.4	3.1
Ryegrass	−31.4	0.097	98.5	1.5	1.9
Spinach	−15.0	0.192	97.5	2.9	3.8
Spring wheat	−18.1	0.271	96.6	4.1	5.4
Winter rye	5.9	0.176	95.8	2.6	3.5
Winter wheat	− 9.3	0.189	88.0	2.8	3.8

[a]Data for depth 5, 10 and 15 cm for leeks were excluded from the regression (see text).

of 8.5 cm day^{-1} (corresponding to 0.53 cm (°C day)$^{-1}$. This is double the rate we found (0.26 cm (°C day)$^{-1}$).

Dardanelli et al. (1997) calculated apparent rooting depth from soil water depletion curves for several crops and derived root front velocities for sunflower, soybean, maize and peanut of 4.4, 3.4, 3.0 and 2.3 cm day^{-1}, respectively. Their rate for maize in cm day^{-1} is higher than indicated in Table 4 but this might be because temperatures were higher in their experiments (20–24 °C).

Thorup Kristensen (2001) reported that monocot species had rooting depth penetration rates in the range of 0.10–0.12 cm (°C day)$^{-1}$ whereas non-legume dicots had rates between 0.15 and 0.23 cm (°C day)$^{-1}$. He estimated that the thermal time needed for the roots to reach a depth of 1 m varied from 750 °C day for fodder radish to 1375 °C day for Italian ryegrass. In our data, the first roots of fodder radish were observed at a depth of 100 cm after 400 °C day. For ryegrass (English ryegrass, not Italian ryegrass) the thermal time needed was 1139 °C day. These lower figures might be related to the optimal conditions for root growth in the Rhizolab.

Rooting characteristics and sustainable cropping systems

In general we are confident that the figures for the crops we used in this study give a good indication of root growth not constrained by physical, physiological or pathogenic factors. As such they can be useful to modellers as a basis for predicting root growth (rooting depth as well as rooting intensity) as function of thermal time after planting. In turn, these models could be helpful in developing fertilisation strategies that try to match crop-available nitrogen as closely as possible to the crop's nitrogen requirements both temporarily and spatially, in order to prevent nitrogen leaching.

Another way of reducing nitrogen losses to groundwater and surface water is to adjust the cropping sequence to take account of the different rooting behaviours of crops. Thorup Kristensen (2002) discussed how crops with different rooting depths can be optimally placed in a cropping sequence in combination with the use of nitrogen catch crops. By growing deep-rooted crops to follow crops that had left much N in the soil in the previous year, the utilisation of the residual N greatly improved; this illustrates the importance of rooting characteristics.

In a paper examining the nature and importance of the dynamics of crop root growth and the practical implications for different (sustainable) cropping systems, Goss and Watson (2003) mention other concepts in which roots play a crucial role. For example, companion crops (living mulch) that grow slowly and flourish as the main crop senesces could be selected in order to extend the period of nutrient removal. Where the interest is in improved soil structure, crops with root systems that provide good anchorage for the plant will also tend to stabilise the surface soil. In general, crops with a rapid production rate are considered valuable for improving soil structure. In the light of these considerations, the knowledge on rooting characteristics presented in this paper could not only aid modellers but also those wanting to improve the options in cropping sequences, nutrient use efficiency and plant performance to meet the demands of sustainable agriculture.

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